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LIFE HISTORIES AND LARVAL BEHAVIOR OF ARRENURID WATER-MITES PARASITIZING ODONATA

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Arrenurus all illustrate an unmodified life history pattern consisting of three active stages: the larva that is parasitic on an adult insect, followed by two free-living aquatic stages, the nymph and adult. The consistent life history pattern of the genus has been thoroughly established in the fine studies of Dr. Paul Münchberg, 1935 et. seq.), but there are many small differences in the details of each species life history that are considered to have great significance in the survival and success of the parasitic larvae and those related to larval attachment are taken up below.

Six life histories are reported and these were reared in the laboratory as a part of the studies of the water-mite fauna of the Edwin S. George Reserve, which is located 2 miles west of Pinckney, Livingston County, Michigan. Grants-In-Aid from the Edwin S. George Scholarship Fund provided support for this work and I am greatly indebted to the late J. Speed Rogers and to T. H. Hubbell who have been responsible for this continued assistance. Much was accomplished in these studies because I did not hesitate to take (and make my own) many suggestions and much labor generously offered by the Curator of the George Reserve, Irving J. Cantrall. Identifications of the dragonflies were checked by Edward J. Kormondy.

INTRODUCTION

Previous records of *Arrenurus* larvae parasitizing Odonata (Münchberg 1935 et. seq.) suggest that each *Arrenurus* has a limited attachment site preference but that species differ widely

in their site selection. As the data reported below were collected, an increasing amount of attention was directed to the relation of attachment site to larval and host behavior. The fact that studies were based on parasites collected on the host, limited the approach to problems encountered by larvae during and after parasitism. Once a larva attaches itself to the host, successful completion of parasitism requires that the larva obtain adequate nutrition and water from the host and be finally reintroduced into a suitable aquatic habitat. Success in both these matters might be related to attachment position and it seems best to outline theoretical speculations as to site selection and then examine the data for correspondences with theory.

Larvae permanently attach themselves to the host by their mouthparts and withdraw nutrients and water through a tube produced in the host tissues (Marshall and Staley (1929; Miyazaki 1936). Any membrane and some sutures appear suitable as attachment sites for the larvae and the fact that extensive membranes of Odonata are ventrally located seems sufficient explanation for the occurrence of most mites on that surface.

Entering a suitable aquatic habitat after riding an odonate imago for several days is an event that may depend on the probability of the host's dying over or in water, in which case the mite larvae could be quite passive after attaching to the host. Some larvae may actively abandon their host but their small size and hydrophobic integument means that they will not easily pass through the surface film. Re-entering the water will be insured if some action of the host introduces into the water at least the part of the body to which the mites are attached, and under such conditions the larvae must be able to release.

Obviously the only predictable entrance of Odonata imagos into the water is during oviposition which occurs in only certain ways in certain Odonata. Immersion of the female, including in some cases the attached male, may be complete (as in some Coenagrionidae) or only the very tip of the abdomen may be dipped into the water (as typical of Libellulidae). Since larvae that abandon their host must be attached to a part of the host body that enters the water, the extent of attachment sites is a function of host behavior. Active larvae must select sites and suitable hosts. The possibility that pseudoviposition may be carried out by some male libelluline dragonflies (Moore, 1952;

Jacobs, 1955) suggests that sexual discrimination of hosts by larvae is not necessary in some cases.

Finally attached mites are quite likely subject to abrasion and injurious blows while attached to the host. Projecting appendages would protect thoracic attachment zones making them most secure, and it would appear that protection would be a factor in site selection.

On purely speculative grounds it is concluded that host and site selection by mite larvae would be influenced by the way larvae re-enter the water, by available nutrient, and by relative protection from injury. The first would require accurate host discrimination and attachment site correlated with host behavior. The last two factors would be nearly constant for all Odonata hosts as to favored sites and would not require host discrimination.

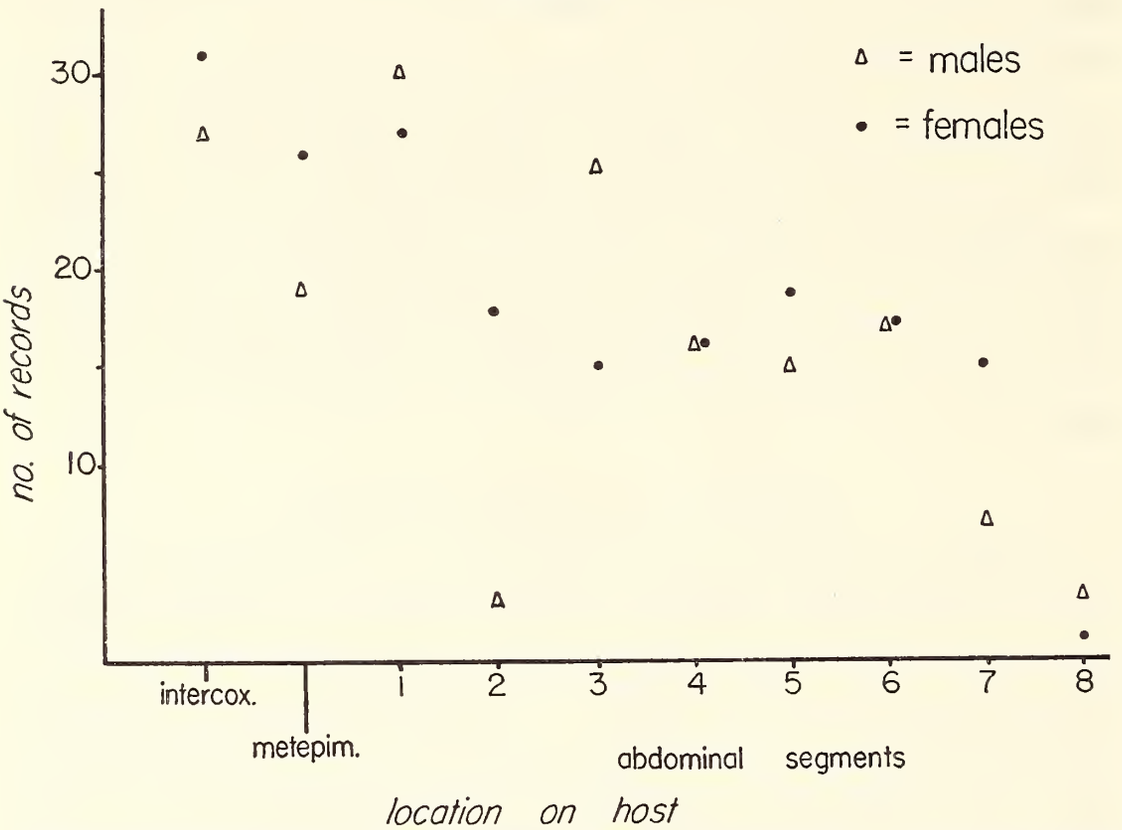
Arrenurus (*A.*) *major* Marshall

A. major is the most abundant species of *Arrenurus* and parasitizes a damselfly, *Ishnura verticalis* (Say) (Coenagrionidae), that is abundant and easily captured. Thus, observations on this parasite are the most complete. During the main flight period of the host, from early June to late August, 90 to 95 per cent of the *L. verticalis* are parasitized by an average of 13 larvae. Münchberg (1951) has already published an outline of this life history.

As long as the larvae are attached to the host and their integument is dry no activity was ever noted, but fully engorged larvae become active a few seconds after being dampened. Their legs move slowly at first but with greater speed and power as time passes, and whenever the legs strike a solid object the mite presses the legs firmly against the host, causing the body of the mite to be pushed back and forth on the attachment of the mouthparts. Evidently the mouthparts, once they are imbedded in the host integument, cannot be freed by their own action and loosen only as the mite larva twists about on that attachment. Most individuals are free of their attachment in ten to fifteen minutes, but a few larvae are never able to free themselves. Active unattached larvae are able to swim away from the host when it is dipped in water, but since their inefficient swimming is not enough to overcome their weight the larvae settle to the bottom where their

swimming movements propel them along the substrate at a speed of about a centimeter a second. The larvae can also crawl upon or cling to plants or algal strands. Activity persists until the nymphochrysalis is formed some 24 to 48 hours after release. If

GRAPH I.



The number of times a given site was found occupied by *A. major* larvae from a sample of 40 *I. verticalis* of each sex collected on July 21, 1957. The sites are the intercoxal membranes, the venter of the meteprimeron, and the venter of the first eight abdominal segments.

possible the larvae will form the nymphochrysalis while grasping or in contact with some object.

There is limited time during which larvae can drop off the host. Larvae not leaving during that time become more engorged and thicker skinned than average and do not become active when moistened, although they transform if the host is kept in water.

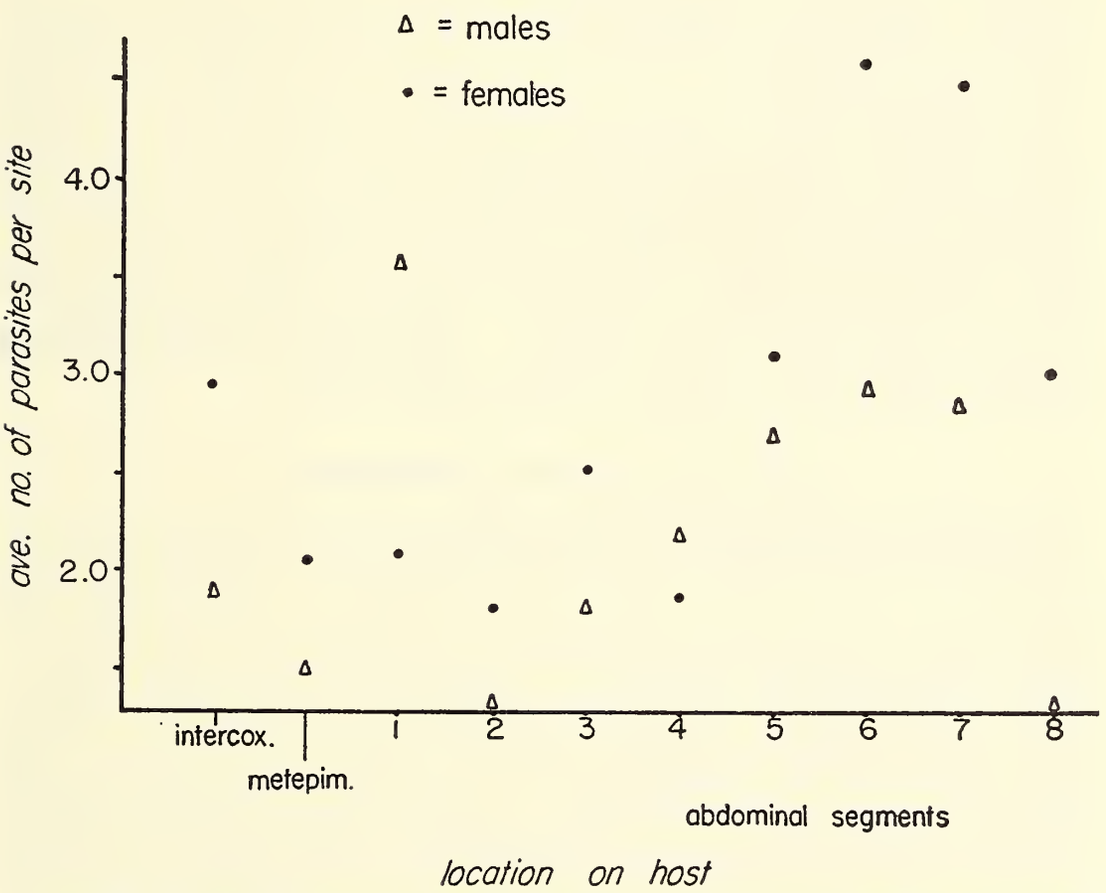
Oviposition by *Ishnura verticalis* involves both male and female. Females often go beneath the surface of the water. Males in tandem may enter the water far enough to wet the abdomen but usually no further (Grieve 1937). Larvae attached to the abdomen will be most likely to have an opportunity to re-enter the water.

Graph I shows the frequency with which larval mites are found

at a given location on the host. Graph II shows the average number found at individual sites for the entire sample. Sexual modifications of the second abdominal segment of the male make it an unsatisfactory site, but in all other respects the graphs indicate no site selection. This may be due to two nearly balanced pressures—one favoring larvae that re-enter the water from abdominal segments and the other favoring larvae that are protected at a thoracic attachment but have fewer opportunities to re-enter the water. A second explanation is that the ability of larvae to remain on the host as passive larvae may make site selection less important.

The nymphochrysalis, which is formed within 48 hours of release of the larva, is of short duration for the nymph emerges

GRAPH II.



Average number of larvae found at each parasitized site taken from the same sample as Graph I.

in two to six days to feed on ostracods or daphnia for a period of two to three weeks after which the teleiochrysalis is formed. Adults emerge from that stage in one to two weeks. Thus, post larval development can take place in just over a month.

Since parasitized *A. major* are found throughout the summer, it is likely that there must be at least two and possibly three overlapping generations each year. Field collections indicated that the adult is probably not a stage that overwinters.

Arrenurus bleptopetiolatus Cook

A. bleptopetiolatus was reared from ten green larvae attached to the venter of abdominal segments 8 and 9 of a male *Epicordulia princeps* Hagen (Libellulidae) collected on June 24, 1957. The response of these larvae to water and their activity was not determined. However, the location of the parasites at the tip of the abdomen suggests that they do drop off at oviposition. After being placed in water the larvae commenced transformation within two days and nymphs emerged in two more days. The nymphs readily ate ostracods and after feeding for just under a month transformed. A week or so later the adults emerged.

The concentration of larvae on the host is just where it would be expected if the parasite assumed an active role in re-entering the water for the oviposition habits of the host are given by Needham and Heywood (1929) as follows: "The female oviposits alone. She descends to touch the water at points wide apart, far out from shore in open water." The fate of mites attached to males would be to ride their host until it dies.

Arrenurus compactilis Marshall

In mid-June both sexes of *Enallagma ebrium* (Hagen) (Coenagrionidae) were often found with as many as ten greenish mite larvae attached to the venter of the metathorax and to the coxal membranes of legs II and III. Larvae taken from this host on June 16, 1957 later developed into adult *A. compactilis*. When these larvae were moistened the legs began to move, at first slowly and later quite vigorously. As the larvae pressed against the host with their legs their mouthparts were loosened so that the larvae were shortly freed from their hold to the host. Once in the water very vigorous actvity of the legs propelled the larva slowly through the water. Within the next 24 hours the larva transformed into the nymphochrysalis from which the nymph emerged in as short a time as three days. Generally the nymphs fed on ostracods, although a few daphnia were taken, and after

three to four weeks' feeding the nymphs entered the teleiochrysalis from which the adult emerged a month later.

Larvae attached to female *E. ebrium* are assured of an opportunity to re-enter the water for the host females descend below the water to oviposit in plant stems (Walker, 1953). There are no reliable data as to how often the male is involved in oviposition or the part he normally takes in the process. In some species of *Enallagma* the male does partially enter the water according to Needham and Heywood (1929).

Owing to the fact that the host is often submerged during oviposition, *A. compactilis* can attach to areas of optimum stability and protection and the thorax appears to be just such a location.

Arrenurus fissicornis Marshall

Often as many as 100 larvae of this mite are found attached only to the venter of the terminal abdominal segments of both sexes of at least three dragonflies of the family Libellulidae. *Libellula incesta* Hagen, *L. luctuosa* Burm., and *Erythemis simplicicollis* (Say). Rearings were made from hosts collected from June 20 to 25, 1957 and during the latter part of June parasitism was nearly 100 per cent. Evidently these dark green larvae did drop off during oviposition, for several old females of *L. incesta* were found with very badly torn intersegmental membranes of the abdomen but with very few mite larvae remaining. In the laboratory, larvae attached to the host would loosen their grip if moistened, although complete release from the host was rarely achieved without some slight external pressure being applied to the mite larva.

Once off the host the larvae were active, but the movements of their legs were ineffectual in propulsion. In two to three days the nymphochrysalis was formed and the nymphs emerged to feed on ostracods for two to three weeks. The nymphs then entered the teleiochrysalis stage from which the adult emerged in about ten days.

Both laboratory observations and the condition of old host females confirm the fact that these mite larvae, which are always found attached to the venter of abdominal segments 5 through 9, must leave the host when the female oviposits. Since larvae did not entirely loosen themselves in the laboratory it might be as-

sumed that as the ovipositing host strikes the water with her abdomen, the larvae which have partially loosened their attachment are knocked off the host. Presumably all three hosts show the typical libellulid oviposition behavior as indicated by Walker (1953) : Many species "oviposit by flying low over the water and striking the surface here and there with the end of the abdomen. . . ." Some pond species may "tap the water with abdomen rhythmically, about four times a second, and always rising between strokes to the same height, five inches."

Arrenurus pollictus Marshall

During most of June three species of *Lestes, L. disjunctus australis* Walker, *L. eurinus* Say and *L. forcipatus* Rambur (Lestidae) were found to be parasitized by reddish mite larvae that were attached to the ventral and lateral sutures of the thorax. *A. pollictus* was reared from these three host species collected from June 16 to 19, 1957. The heavily engorged larvae did not react when moistened and even when removed from the host and placed in water still showed no activity. Transformation commenced within 24 hours of removal of the larvae from the host and the nymphs emerged in 4 to 5 days to feed on both daphnia and ostracods. After a month of feeding the teleiochrysalis was formed from which the adult emerged in a few days.

Most species of *Lestes* oviposit in stems over the water (Walker 1953), although *L. forcipatus* is among the exceptions to the rule and oviposits at or under the water surface (Needham and Heywood 1929). Certainly the majority of the mites attached to these hosts only re-enter the water if the host dies over water. Larvae of this mite attach to the stable, well-protected venter of the thorax and, when engorged, lose all ability to move.

Arrenurus tetratumuli Münchberg

This species was described from undeveloped males reared by Münchberg from *Erythemis simpicicollis* (Say) and *Pachydiplax longipennis* (Burm.) (Libellulidae) collected at Point Pelee, Ontario. (Münchberg 1953). Features of the petiole were not developed in the type series and Dr. Münchberg has very kindly compared the male of *A. tetratumuli* with these specimens. Doctors Cook and Münchberg agree that *A. neosuperior* must

be synonomized with *A. tetratumuli.* Cook (1954) adequately illustrates and describes, under the name *A. neosuperior,* the differentiating characters of the entity that must go under the name *A. tetratumuli* Münchberg.

One parasitized specimen of *Pachydiplax longipennis* was collected on July 28, 1956 and found to have a few scattered very dark green larvae attached to the ventral region of the metathorax. On removal from the host the larvae showed no signs of activity in water but, within a few days, had transformed. The nymphs emerged in two weeks and fed on daphnia. On completion of the nymphal stage two males and four females emerged. These details of biology are in complete accord with the facts reported by Münchberg (1953).

Both the libelluline hosts reported for the species probably oviposit in the typical libellulid fashion with only the female involved. She merely dips the tip of the abdomen in the water during flight and releases eggs each time the abdomen strikes the water. Hence larvae attached to the thorax, as is the rule in *A. tetratumuli* will not be able to re-enter the water. Observations in the laboratory indicate that this larva does not respond to moistening and must passively depend on the host's drowning or dying over water in order to complete the life cycle.

Arrenurus wallensis Cook

Throughout late June and July, *Celithemis eponina* (Drury) and *C. elisa* (Hagen) (Libellulidae) are commonly parasitized by two types of larvae; a bright red larva that attaches to the lateral sutures of the meso- and meta-thorax, and a dark green larva that is almost always attached along the V-shaped suture of the ventral surface of the meteprimeron where, if crowded, the mite larvae form two neat rows alternating with each other. Only the green larvae have been reared out. These are discussed below.

Arrenurus wallensis was reared from dark green larvae removed from the venter of the metathorax of *Celithemis eponina* collected on July 28, 1956. The larvae did not drop off the host when moistened. When removed and put in water they were inactive, and the nymphochrysalis was formed immediately. After ten days the nymphs emerged and readily fed upon daphnia until entering the brief teleiochrysalis stage some six weeks later.

About 20 fully engorged larvae occupy all the available space on the suture and only rarely attach to metepimeral sutures. Newly emerged dragonflies bear more than twenty mites, which suggests that the limited numbers and precise arrangement of engorged individuals is the result of competition that permits maturation of only those larvae that are properly placed on the suture. Since the limited attachment sites are not related to larval release, and occasional individuals attached to lateral thoracic sutures do feed and mature, it has not been possible to explain the limitations seen in the parasitism.

CONCLUSIONS

Odonata were found with mite larvae attached to ventral membranes from the mesothorax to the ninth abdominal segment with each mite species usually limited to one small area on the host. Protection is the only factor that need influence the attachment site of passive larvae which re-enter the water on the death of the host over or in the water. Inactive larvae such as *A. wallensis, A. pollictus,* and *A. tetratumuli* seek a thoracic attachment where the most protection is to be had.

The so-called active release of mite larvae from their attachment to the host may completely free the mite from its attachment or only loosen the attachment so that external forces easily free the larvae. This release was only seen after moistening and, unless moistened, attached larvae were quiescent. If an engorged mite did free itself from the host, directed locomotion was impossible and the mite either remained in place or dropped off the host. Thus, all mites that responded to wetting were found attached to parts of the host that were likely to be moistened. Parasites of hosts that dip the tip of the abdomen in water at oviposition must be concentrated on the tip of the abdomen as in *A. bleptopetiolatus* and *A. fissicornis.* Parasites of hosts that enter the water during oviposition have a wider range of potential attachment sites, but in these cases factors related to protection can restrict site selection by the larvae, as appeared to be the case in *A. compactilis.*

In its lack of any pronounced site selection, *A. major* represents an unsolved problem. Two possible explanations are offered above, both of which conform with the general views expressed here.

While *Arrenurus* are, for the most part, quite specific in their site of attachment they are often unspecific in their host selection. Many instances of apparent host specificity could be the result of only one potential host being available in the habitat. *A. planus,* a parasite on the thorax of both Anisoptera and Zygoptera (Münchberg 1952) is a most impressive case of wide latitude in host selection but restricted site selection. Larvae that take an active part in leaving the host are found to be limited to hosts of similar oviposition habits and it is noteworthy that there is no sex differentiation on the part of the larvae. The parasites on males may be lost, simulated oviposition by males may be common (Moore 1952, Jacobs 1955), or larvae may be able to live through the active life of the host and return to the water if the host dies over the water. Thus, the absence of sex selection in active parasites may mean that leaving the host at oviposition is only one of several ways by which parasites of one species may re-enter the water.

While only a few instances are considered here, it appears that host and site selection by *Arrenurus* larvae are best explained in terms of factors favoring the survival and re-entry of larvae into the water.

References

COOK, D. R. 1954. Preliminary list of the Arrenuri of Michigan. Part I. The subgenus *Arrenurus*. Trans. Amer. Mic. Soc. **73**: 39–58.

GRIEVE, E. F. 1937. Studies on the biology of the damselfly *Ishnura verticalis* Say, with notes on certain parasites. Ent. Amer. **17**: 121–152.

JACOBS, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology. **36**: 566–586.

MARSHALL, J. F. AND J. STALEY. 1929. A newly observed reaction of certain species of mosquitoes to the bites of larval hydrachnids. Parasitology. **21**: 158–160.

MIYAZAKI, ICHIRO. 1936. Über das Saugorgan von zwei Arten Wassermilbenlarven. Annot. Zool. Jap. **15**: 306–308, pls. 17–18.

MOORE, N. W. 1952. Notes on the oviposition behavior of the dragonfly *Sympetrum striolatum* Charpentier. Behavior. **4**: 101–103.

MÜNCHBERG, PAUL. 1935. Zur Kenntnis der Odonatenparasiten, mit ganz besonderer Berücksichtigung der Öcologie der in Europa an Libellen schmarotzenden Wassermilbenlarven. Arch. Hydrobiol. **29**: 1–120.

———. 1951. Ein zweiter Beitrag über die in den USA. eine odonatenparasitische Larvenphase aufweisenden *Arrenurus*-Arten (Ordnung: Hydracarina) Arch. Hydrobiol. **45**: 378–388.

———. 1952. Über Fortpflanzung, Lebensweise und Körperbau von *Arrenurus planus* Marsh., zugleich ein weiterer Beitrag zur Ökologie

und Morphologie der im arctogäischen Raum eine libellenparasitische Larvenphase aufweisenden *Arrenurui* (Ordunug: Hydracarina). Zool. Jahrb. (Syst.). **81**: 27–46.

————. 1953. Vierter Betrag zur Kenntnis der nordamerikanischen Raume an Odonaten parasitierenden *Arrenurus*-Arten (Ordnung: Hydracarina). Zool. Jahrb. (Syst.). **82**: 47–57.

NEEDHAM, J. G. AND H. B. HEYWOOD. 1929. A handbook of the dragonflies of North America. 8 + 378 pp., C. C. Thomas, Springfield, Ill.

WALKER, E. M. 1953. The Odonata of Canada and Alaska. **1**. 11 + 292 pp. Univ. of Toronto Press.